Removal of intertidal grazers by human harvesting leads to alteration of species interactions, community structure and resilience to climate change

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ABSTRACT

Extreme fluctuations in abiotic conditions can induce a biological stress response (e.g. bleaching) detrimental to an organism's health. In some instances, organisms can recover if conditions are alleviated, such as through co-occurrence with other species that confer protection. Biodiverse, multitrophic communities are increasingly recognised as important promoters of species persistence and resilience under environmental change. On intertidal shores, the role of grazers as top-down determinants of algal community structure is well recognised. Similarly, the harvesting of grazers for human consumption is increasingly prevalent with potential to greatly alter the community dynamics. Here, we assess how differences in harvesting pressure of grazers under three management regimes (no-take; managed access; open-access) alters the trophic interactions between grazers, and algal communities. Grazer density and body size frequencies were different among regimes leading to changes in the photosynthetic performance and recovery of crustose coralline algae (CCA) post-bleaching, as well as their presence altering the strength of interactions between species. The exclusion of grazers from patches using cages led to different emergent communities and reduced negative correlations between taxa. The absence of larger grazers (> 9 cm) at the managed access site led to macroalgal overgrowth of bleached CCA negatively affecting its recovery, whereas no-take or open-access led to a moderated algal growth and a shift from competitive to facilitative interactions between algal species. Given that CCA play an important role in the population growth and development of other species, the choice of management measure should be carefully considered before implementation, depending on objectives.

1. Introduction

Climate change is expected to increase the intensity and frequency of extreme weather events (Field et al., 2012) affecting marine ecosystems and the economies and societies that depend on them (Harley et al., 2012). In addition to the background of gradual ocean warming (a 'press' perturbation), temporally brief but extreme departures from typical conditions ('pulse' perturbations) can lead to significant disruptive stress for many organisms that may severely affect the functioning of biological systems (Russell et al., 2009). For intertidal organisms, the combination of low tides, calm seas, elevated air temperatures and high solar radiation (UV) may act as short-term, but extreme departures from typical conditions causing severe and widespread damage or mortality (e.g. Bender et al., 1984).

Bleaching of corals (Ampou et al., 2017) and algae (Hawkins and Hartnoll, 1985; Scrosati and DeWreede, 1998; Wieters et al., 2013) are particularly clear biological stress responses associated with exposure to anomalous environmental conditions (Brown, 1997). Manifested as the loss of symbiotic zooxanthellae or damage to photosynthetic pigments (Davison and Pearson, 1996), bleaching events are occurring worldwide at historically unprecedented rates (Anthony, 2016) leading to marked reductions in primary productivity (Harley et al., 2012; Irving et al., 2004; Kayanne et al., 2005), and negative impacts on food web structure and ecosystem functioning (Graham et al., 2015).

Recovery following bleaching is, however, possible if stressful conditions are alleviated (Baker et al., 2008). Stress may be alleviated in several ways including individual behavioural responses, such as physical relocation, that limit the duration of exposure to detrimental environmental conditions (Littler, 1972), or associational defences whereby other co-occurring species provide protection (Irving et al., 2004). Increasingly, the importance of biologically-diverse, multi-trophic communities is being recognised as a mechanism for species

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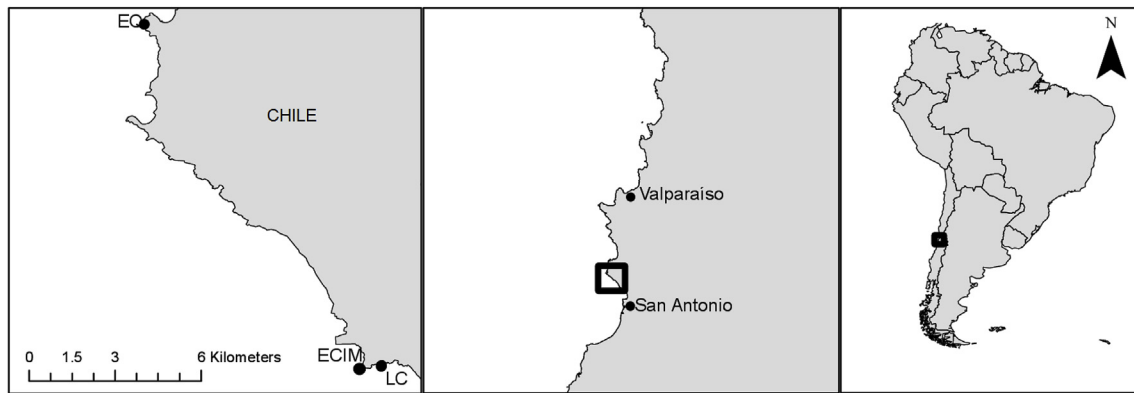 *E-mail address:* aknights@plymouth.ac.uk (A.M. Knights).

Fig. 1. Location of the three experimental sites: Estación Costera de Investigaciones Marinas (ECIM) - no-take marine reserve; Las Cruces (LC) - open access harvest area; and El Quisco (EQ) – managed access area.

persistence in environments that ordinarily would be stressful to an individual (Griffin et al., 2009; Steiner et al., 2006). For instance, in intertidal systems, crustose coralline algae (CCA) can compete for resources with turf-forming algae or macroalgal canopy species that can reduce the availability of light by shading (Irving et al., 2004). However, 'shading' has also been shown to limit damage to CCA from high irradiance levels by reducing the risk of desiccation (Figueiredo et al., 2000; Melville and Connell, 2001). Competitors may therefore act as 'buffers' against environmental change, facilitating the persistence of individuals (e.g. see Przeslawski and Benkendorff, 2005; Wahl et al., 2004 and Bulleri et al., 2018 for examples in other taxa) and entire assemblages via the provision of refugia from environmental stress. The role of facilitation is increasingly recognised as enhancing food web topology and stability by reducing the strength of negative competitive interactions (Rooney and McCann, 2012), and enhancing species fitness (Bertness and Callaway, 1994; Leonard, 2000).

On intertidal rocky shores, it has long been known that grazers can play a critical role in reducing algal biomass (Steneck, 1982; Wanders, 1977), preventing recovery from a bleaching event. Grazers have been shown to prevent colour restoration through the removal of epiphytes that provide shade (Figueiredo et al., 2000). The size and density of grazers has also been correlated with changes in algal biomass loss, with higher densities of large grazers reducing algal biomass, which in turn, reduces the abundance of healthy CCA (Cattaneo and Mousseau, 1995). In many areas, intertidal grazers important in controlling the abundance and distribution of algae are removed by humans for food (Espinosa et al., 2014; Moreno et al., 1984). Large-scale changes in the population structure, size distributions and density of grazers can occur (Oliva and Castilla, 1986) in turn, directly affecting lower trophic levels (Paine, 1980; Polis et al., 2000) and indirectly affecting the entire system by decoupling fast (small, fast growing populations with high biomass turnover and strong interactions) and slow (low biomass turnover and weak community interactions) energy channels (Rooney and McCann, 2012). The most profound change directly mediated through harvesting is highlighted on rocky shores where the removal of grazers often leads to algal proliferation (Moreno et al., 1984; Oliva and Castilla, 1986). The effect of top-down pressure from predators including humans on grazer densities can therefore alter the outcome of conservation efforts that directly or indirect influence grazer assemblages with knock-on consequences for primary producers including CCAs (O'Leary and McClanahan, 2010; Paine, 1980; Polis et al., 2000).

Efforts to balance biodiversity conservation with sustainable harvesting practices are on-going worldwide (Espinosa et al., 2014). Conservation strategies like Marine Protected Areas (MPAs) can result in altered demographic structure of populations, influencing species size distributions and the density of grazers (Oliva and Castilla, 1986), and indirectly influencing lower trophic levels via top-down cascading effects (O'Leary and McClanahan, 2010; Paine, 1980; Polis et al., 2000),

especially algae (Moreno et al., 1984; Oliva and Castilla, 1986). The level of protection afforded to species and habitats within a reserve can, however, vary depending on the reserve objectives (Lester and Halpern, 2008; Lester et al., 2009). In some instances, this is complete protection (no-take) for all species; in others, partial protection (restrictions) for certain species or control of activities considered harmful (Knights et al., 2015; Piet et al., 2015). Differences in the level of protection can result in emergent communities with varying structural (biomass, density, diversity) and functional (trophic interactions) properties depending on the type of reserve implemented (Lester and Halpern, 2008). It is therefore difficult to differentiate the effect of conservation strategies from the natural biological structuring of communities due to changes in multitrophic species interactions.

Here, we explore how different management objectives can alter multitrophic interactions among humans (harvesting), grazers, macroalgae, and crustose coralline algae (CCA). We explore the extent to which changes in harvesting pressure associated with different ecosystem management measures alters the structure of the grazing community, and by way of a series of cage experiments, make links between the effect of harvesting and the capacity for primary producers (i.e. CCA) to withstand pulse perturbations associated with intertidal living.

2. Materials and methods

2.1. Study sites

Experiments were conducted at three wave-exposed rocky intertidal sites of relatively weak upwelling along the coast of central Chile (Fig. 1). Estación Costera de Investigaciones Marinas (ECIM) is a no-take marine reserve established in October 1982, covering approximately 500 m of rocky shore and 10 ha of subtidal rocky reefs. Immediately adjacent, Las Cruces (LC) applies seasonal closures but otherwise access and harvesting is unrestricted, while, 18 km north, El Quisco (EQ) is a territorial users rights fisheries management area (MA) assigned by the government to the Fishermen's Union in 1993. The fishing union works alongside marine ecologists to develop a management plan and conduct annual assessments to assess and set changes in the total allowable catch of benthic resources and minimum size limits for harvested species (Gallardo Fernández, 2008).

Across the three sites, epibenthic communities of the low intertidal zone are characterised by canopy kelp (*Lessonia* and *Durvillaea antartica*), crustose (mostly *Hildebrandia* spp.) and calcified coralline (*Lithothamnion* spp.) and corticated algae (*Gelidium* spp.) as well as mobile consumers including patellid gastropods (*Scurria*), chitons (predominantly *Chiton granosus*) and keyhole limpets (*Fissurella* spp.) (Broitman et al., 2001).
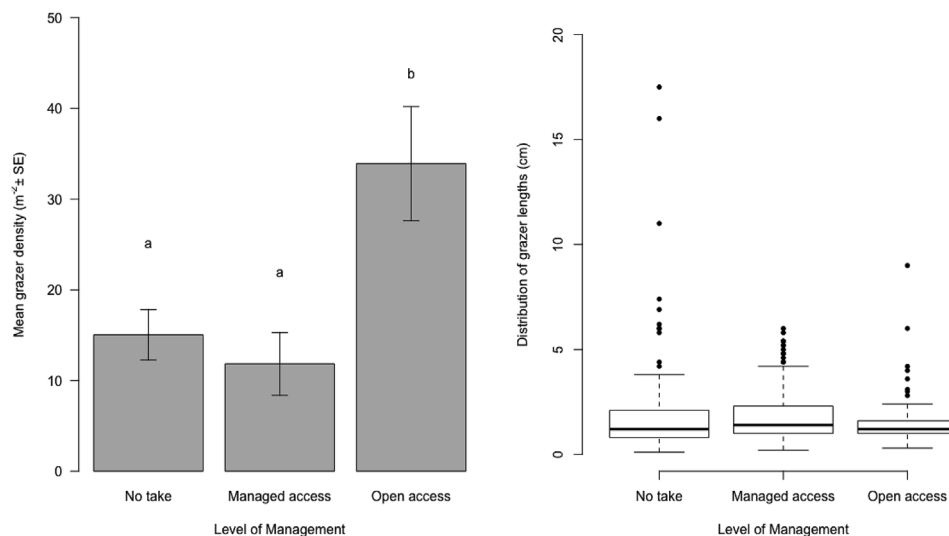
Fig. 2. (a) Mean (± S.E.) grazer density, and (b) distribution of body lengths of intertidal grazers at three sites with differing management regimes. Different letters above bars indicate significant differences (p < 0.05) between groups as revealed by Tukey *post-hoc* tests.

2.2. Experimental design and set-up

Biodiversity management tools, such as marine MPAs, are largely absent throughout Chile (see www.mpatlas.org for a review) curtailing our ability to 'replicate' this study across management regimes. As such, this study undertakes an exploratory comparison of the three locations, describing the community structure and associated changes in structure and functioning in each following our experiment, rather than attempting to formally compare management strategies by including 'management' as a factor in our analyses. Instead, we compare sites, either in a one-factor analysis (i.e. grazer density and length), or as a random factor (photosynthetic yield and percentage cover analyses) to test the null hypothesis of no difference among sites. Any differences were thus inferred to be a result of management rather than direct causation.

To test the effect of grazers on CCA bleaching, cages were used to

exclude potential algal grazers from patches of bleached CCA (BCCA hereafter) and the recovery of the BCCA to healthy CCA (HCCA) was assessed over time. Cage treatments were compared with open (full-access) and procedural controls to test for artefacts of the cage (e.g. Knights et al., 2015). At each site, up to fifteen 225 cm² independent patches containing BCCA were randomly assigned in equal numbers to one of three treatments (control, cage or procedural control). For the cage treatment, square cages (15 × 15 × 3 cm) made of metal mesh (~1 cm diameter) were placed over each BCCA plot once all grazers were removed. Control and procedural control plots, which allow full access by grazers, were identified using screws and tags to indicate the corners of each experimental patch. The procedural control used the same cage material, but only half of the structure was installed to allow grazer entry. The number of replicates in each treatment was limited by the number of naturally-occurring BCCA plots and site restrictions, such that 3, 4 and 5 replicates of each treatment were established at ECIM,
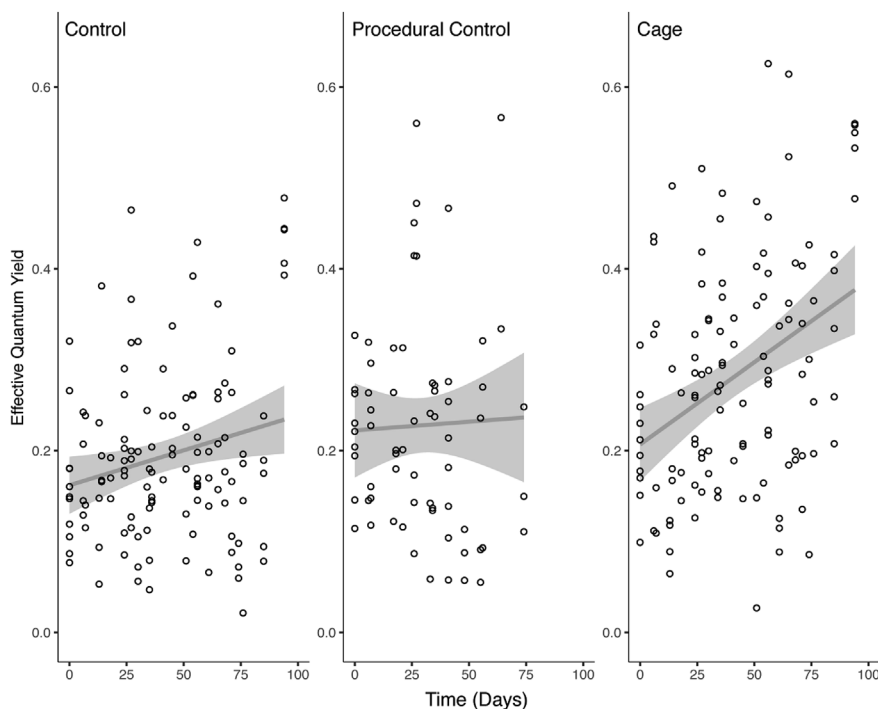

Fig. 3. Change in effective quantum yield (Y) from CCA over time grouped by cage treatment. Significant linear regressions are shown as solid lines. Shading indicates 95% confidence interval. Regression line equations are: Control ($Y_{control} = 0.00077x + 0.16$), Procedural Control ($Y_{cage} = 0.0001x + 0.22$), and Cage ($Y_{cage} = 0.0018x + 0.21$).
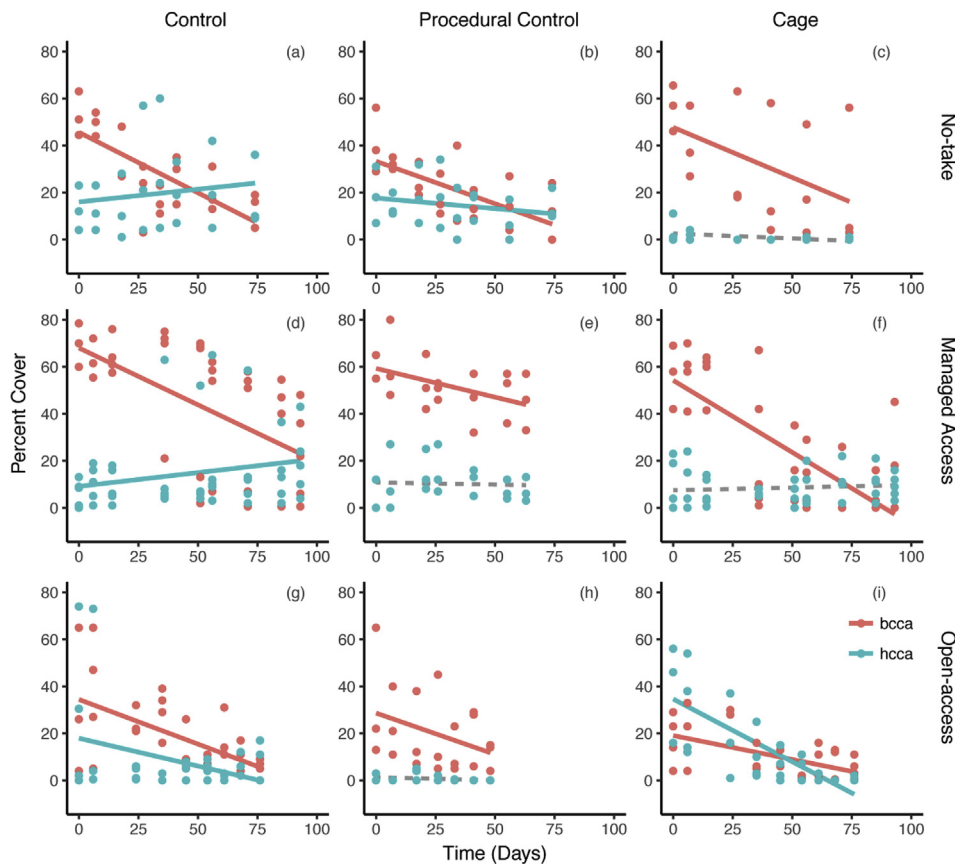
Fig. 4. Percentage of CCA that is healthy (green) or bleached (red) over time (days) in control, procedural control, and cage treatments at sites with different management. Significant linear regressions are shown as solid lines (p < 0.05). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

LC and EQ respectively (for a total of 36 plots). Cages were installed in November 2015 and were monitored for up to 104 days.

2.3. Grazer density and length

Due to differences in harvesting restrictions among sites, density and sizes of individual grazers potentially affecting local algal assemblages was expected to differ. To evaluate this, 25 quadrats (0.25 m²) were haphazardly placed in the low intertidal zone. For each quadrat, the density of all grazers, including *Fissurella* spp., *Scurria* spp., *Siphonaria* spp. and several chiton species (e.g., *Chiton* spp. and *Enoplochiton niger*) was determined, and the shell length (greatest distance between anterior and posterior ends) of all individuals was measured using Vernier callipers.

2.4. Photosynthetic performance

Point measurements of effective quantum yield (Y) from each CCA patch were carried out weekly for the duration of the experiment using a DIVING-PAM fluorometer (Walz, Germany) to evaluate changes in CCA photosynthesis-II between treatments over time. Effective quantum yield was determined by the following (Genty et al., 1989):

$$Y = (F'_m - F)/F'_m$$

where: F_m is the maximal fluorescence yield in a light-adapted plant following saturating-light pulse and F is the normal fluorescence in the light (see Harrington et al., 2005). All point measurements were collected under ambient light with the main optical fibre placed at a distance of 10 mm from the CCA at an angle of 60° to avoid shading or darkening (Beer et al., 1998). To ensure that photosynthesis of CCA alone was measured, a small brush was used to clear epiphytic growth from three small, randomly selected areas on the surface of CCA immediately before measurements (Short et al., 2014).

2.5. Percentage cover

In the first 3 months of the study when algal overgrowth and density did not inhibit photographic analyses, a photograph of each plot was taken weekly and the percentage cover of BCCA and HCCA along with other algae present in the plot were estimated using the image analysis software ImageJ (Abramoff et al., 2004). After 3 months, algal overgrowth made such image analyses difficult and therefore percentage cover was estimated in the field using point sampling. Percentage covers of habitat/species were pooled into one of 11 functional groups based on morphology and resource-use strategies (see Broitman et al., 2001). Estimates of bleaching intensity were calculated as the percentage of CCA cover that was visually bleached and thus was independent of local abundance.

2.6. Data analysis

2.6.1. Grazer density and body size

All data analyses described were performed using the open source software, R (R Development Core Team, 2017).

Grazer densities and body size among sites were compared using one-way ANOVA and Kruskal-Wallis tests respectively. For ANOVA tests, homogeneity of variance was tested using Levene's test and data square-root transformed where relevant to remove heterogeneity. Where significant differences were identified, Tukey HSD *post-hoc* pairwise comparisons were used to identify significant differences between groups.

2.6.2. Change in photosynthetic performance and percent cover of CCA

A linear mixed effects model testing change in (i) photosynthetic yield, and (ii, iii and iv) percentage cover of bleached, healthy and total cover of CCA in different treatments (control; procedural control; cage) with site included as a random factor was developed. Model reduction
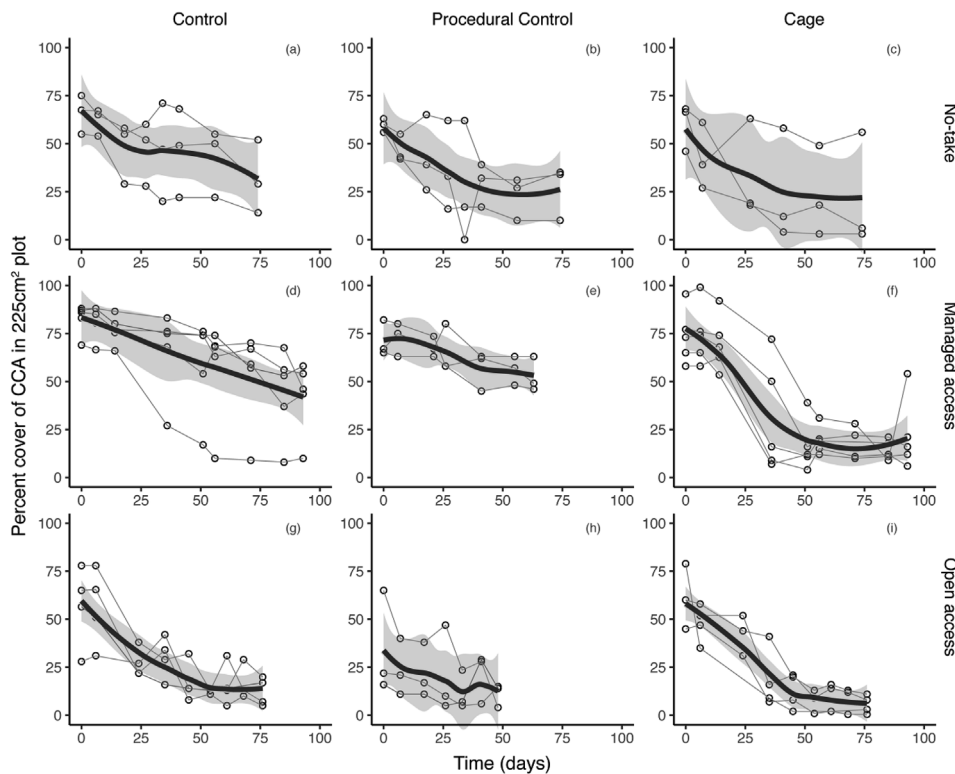
Fig. 5. Change in total percent cover of CCA per 225 cm^2 plot in control, procedural control and caged treatment plots over time. Regressions lines show moving-average with an AR1 correlation structure and associated 95% confidence intervals (shaded area). Light grey lines trace change in percent cover of individual CCA plots.

was undertaken (using AIC goodness of fit comparisons) to reveal the best-fitting model. For photosynthetic yield, this was a generalised least squares (GLS) additive model with an autoregression-moving average correlation structure (AR1) excluding site as a factor, and for percentage cover, this was the maximal (lme) model including site as a factor and also updated to include an autoregression-moving average correlation structure (AR1). Linear regression was used to test for significance of model fit slopes and intercepts for each percent cover estimate of HCCA and BCCA (Fig. 4). Moving-average (localised regression) was used to illustrate change in total percentage cover of CCA over time by site and treatment (Fig. 5).

If CCA recovers, a negative correlation in the percent cover of CCA classified as 'bleached' or 'healthy' was predicted. However, overgrowth by other algae may also occur on the surface of BCCA, so that the percentage cover of HCCA may not return to pre-bleached levels. Using data from the last time point, percentage cover of BCCA was correlated against the percentage cover of HCCA and functional algal groups to assess if BCCA is replaced by other algal species in the presence or absence of grazing pressure. Pearson's correlations are presented using correlation matrices (corrplot package; Friendly, 2002).

To test if local consumer treatment affects the composition of algal communities, permutational multivariate analysis of variance (PERMANOVA; McArdle and Anderson, 2001) and non-metric multidimensional scaling (nMDS) was used with functional groups as variables. PERMANOVA was conducted using the *adonis* function (vegan package; see Oksanen et al., 2016), and where significant results were found, similarity of percentages analysis (Clarke and Warwick, 1998) was used to determine the functional groups most responsible for dissimilarity in community composition. nMDS (conducted using *vegdist* with the Bray-Curtis index of similarity) was used to graphically portray similarity/dissimilarity function in the vegan package. Environmental fitting (*envfit* procedure in vegan) was used to indicate correlation between the time vector and factor centroids.

3. Results

3.1. Grazer density and length

Grazer density was significantly different among sites ($F_{2,72}$ = 7.23, $p < 0.001$) with post-hoc pairwise comparisons revealing a significantly higher grazer density (2.5 x greater) at the open access site (LC), compared with the managed access sites of ECIM and EQ (Fig. 2a). While densities were marginally higher at the no-take reserve site (ECIM) than the fisher-managed MA site (EQ), the difference in total grazer density was not statistically significant. There was no significant difference in median grazer body length at different sites ($F_{2,377}$ = 1.95, $p = 0.15$, Fig. 2b) although at the no take site (ECIM), a number of considerably larger individuals were recorded that were not present at the open-access and managed-access sites (Fig. 2b). The maximum recorded size at ECIM was 17.5 cm, largely contributed by *Fissurella* spp., whereas largest sizes in the managed access and open access sites were 6 and 9 cm respectively.

3.2. CCA recovery of photosynthetic capacity

Changes in photosynthetic yield over time were dependent on treatment and time ($F_{2, 302}$ = 3.2, $p < 0.05$). There were significant differences in the rate of increase in quantum yield over time between 'cage' treatments excluding grazers, and 'control' or 'procedural control' treatments ($p < 0.05$) allowing access to grazers (Fig. 3). Quantum yield increased $2.3x$ faster in caged treatments (a rate of 1.8×10^{-3} ¥ per day) than in the control treatments (7.7×10^{-4} ¥ per day). There was no significant difference in quantum yield over time between control and procedural control treatments, nor any difference in initial quantum yield between treatments (mean yield at Day 0 for all treatments = 0.19 ± 0.07).

3.3. Change in ratio of healthy and bleached CCA over time

The percentage of CCA that was bleached was dependent on site

(AIC fit), treatment ($F_{2,266} = 3.92$, $p < 0.05$; Fig. 4), and time ($F_{1,266} = 267$, $p < 0.001$; Fig. 4). Analysis and subsequent *post-hoc* tests revealed that the percent of bleached CCA at the managed access site (EQ; 42%) was approximately 2.5x and 1.7x greater than at the open access site (LC; 16%) and no-take site (ECIM; 25%) respectively (Fig. 4). The percentage of CCA bleached was ~1.5x greater at the no take site than the open access site. The percentage of bleached CCA decreased significantly over time at a mean rate of 4.3% day^{-1}, irrespective of treatment ($F_{1,266} = 267.2$, $p < 0.0001$; Fig. 4).

Change in percentage cover of healthy CCA was dependent on site, and varied among treatments over time ($F_{2,268} = 5.18$, $p < 0.01$) and varied idiosyncratically. The percentage cover of HCCA increased in the control treatment at the no-take and managed access sites only (Fig. 4a, d). In three other treatments (control, procedural control and cage depending on site), percentage cover of HCCA declined (Fig. 4b, g and i) at a mean rate of ~0.3% cover per day. In the remaining four treatments (Fig. 4c, e, f and h), there was no change in the percentage cover of HCCA over time.

In all plots, there was a reduction in the total areal extent of CCA at all sites over time depending on treatment ($F_{2,534} = 3.40$, $p < 0.05$) (Fig. 5). At the managed site, the exclusion of grazers led to greater reductions in cover (e.g. mean loss of 73% at the managed access site, Fig. 5f), in comparison to plots with grazers (e.g. mean loss of 49% at the managed access site, Fig. 5d). Change in extent over time at the no-take site was more variable among plots than at the managed and open access sites, irrespective of treatment. This was especially true in the cage treatment where individual plots displayed significant reductions or little change in cover over time (Fig. 5c).

3.4. Community analyses

Both positive and negative correlations were found between HCCA, BCCA and other sessile functional groups at each site (Fig. 6), although relatively weak relationships were observed at the open access LC site. At all sites, HCCA and especially, BCCA, were negatively correlated with the abundance of corticated, ephemeral and/or fleshy crustose algae. The most consistent and distinctive pattern of relationships was observed where consumers were excluded: here, strongest negative correlations of BCCA and HCCA were associated with ephemeral algae

at all sites. In contrast, where consumers were present (control and procedural control treatments), relationships were more variable among sites and strong negative correlations of BCCA and/or HCCA were associated with either fleshy crusts and filter feeders (no-take, ECIM), corticated and ephemeral macroalgae (managed access, EQ), or filter feeders (open-access, LC) (Fig. 6). There was only a weak negative correlation between HCCA and BCCA suggesting limited evidence of recovery of BCCA at all sites.

The emergent communities were different among sites, treatments and time (3-way interaction term, F-perm$_{4, 251} = 2.25$, $p < 0.01$) (Fig. 7). Adding terms sequentially, site accounted for the greatest variability in composition (15%), followed by treatment explaining a further 5% of the variance (Fig. 7). Time (R^2, $p < 0.001$) played was a relatively important determinant of emergent community structure at each site, explaining ~21% of the variation in composition. SIMPER analysis revealed differences in algal functional groups between cage and control treatments (65.5% overall dissimilarity) driven by differences in ephemeral (cage plots (Δ) at all sites showed a transition toward a prevalence of ephemeral algae over time), BCCA and corticated algae (Table S1, Fig. 7). Procedural control and control plots showed broadly similar communities. The communities at each site were characteristically different in terms of composition. The no-take site (ECIM) were 61% different from those at the managed site (EQ), and 76% different from the open access site (LC), with certain functional groups more strongly associated with each site (Fig. 7). Biggest differences were driven by the presence/absence of non-calcareous crustose algae and BCCA at the managed site, and by corticated and non-calcareous crustose algae at the open access site. Communities at EQ and LC were 69% different, driven by differences in BCCA and corticated algal abundance (Table S1).

4. Discussion

Current rates of resource exploitation are widely considered unsustainable (Airoldi and Beck, 2007; Halpern et al., 2008) and efforts to find conservation/sustainable solutions ever increasing (Fernandes et al., 2005). The application of no-take areas that set aside areas of the marine environment in which extraction activities are prevented (Hughes et al., 2003) are advocated but when implemented have shown
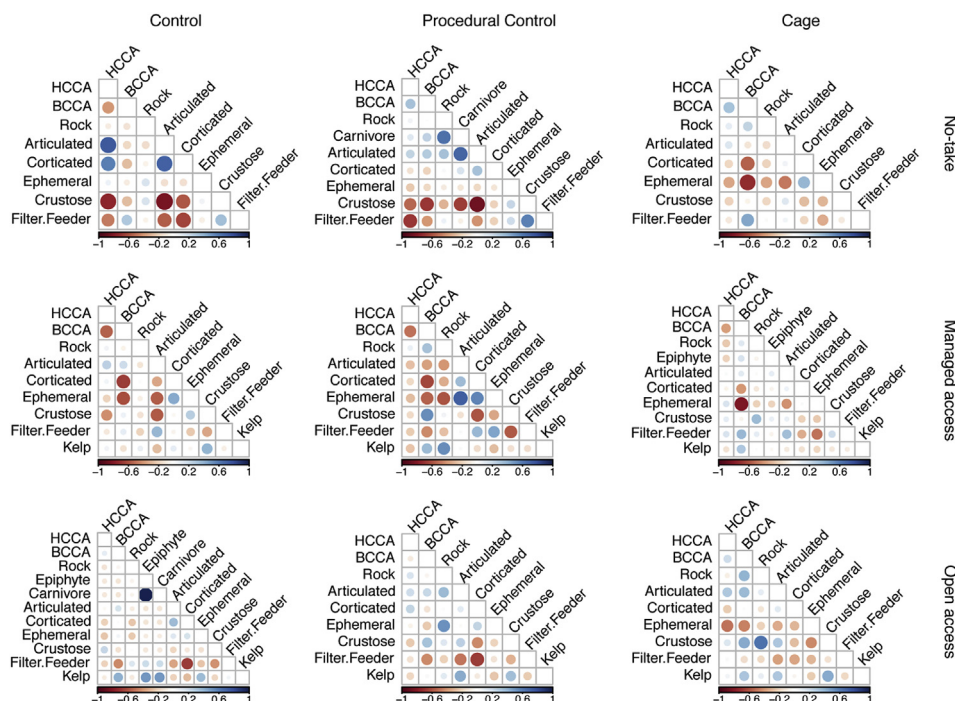

Fig. 6. Correlation between functional groups at the no-take (ECIM; top row), managed access (EQ; middle row) and open access (LC; bottom row) sites. Colour (positive or negative) and circle size (numeric value) indicates the strength of correlation. Only functional groups recorded at each site are shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
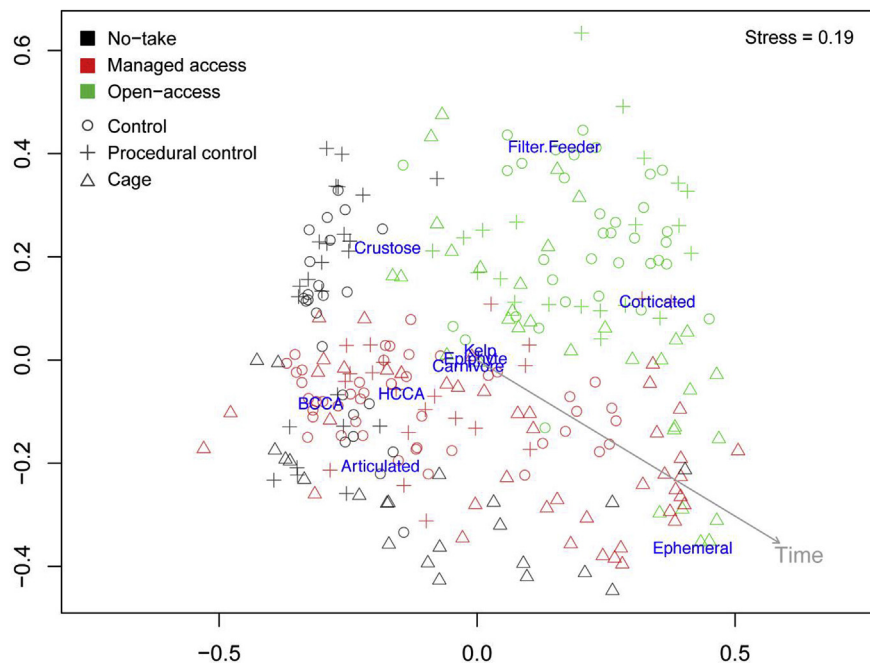
Fig. 7. Dissimilarity in community assemblages based on percentage cover data at each site (indicated by colour points). Text labels indicate the centroid for each taxon and the arrow indicates the strength and direction of correlation between community composition over time ($R^2 = 0.21$, p. < 0.001). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

limited success (Airame et al., 2003). Alternatively, the use of 'customary practice' management (Johannes, 2002) that is utilitarian in aim, is also common place using approaches such as the temporary closure of areas to restrict harvesting (Aswani and Weiant, 2004) in an effort to improve yields (Cinner et al., 2006). In Chile, there is a notable absence of biodiversity conservation measures, like MPAs (www. mpatlas.org), and consequently, a paucity of studies describing their potential value to conservation objectives. Here, we examined differences in the structure of marine communities, and in particular, change in the health of crustose coralline algae at three locations where three different management regimes have been employed (no-take, managed access (i.e. customary management), and open access) to restrict human harvesting of a variety of benthic resources, particularly gastropods.

Unexpectedly, we found that grazer densities in no-take and managed access sites were considerably lower than at the open-access site despite management restrictions. While the median size was not significantly different among locations, a number of larger individuals were apparent at the no-take site while smallest individuals were recorded at the open-access site. An inverse relationship between size and abundance is well documented in a range of taxa (Damuth, 1981; White et al., 2007) although this relationship is often not shown in no-take reserves. For instance, in fish, reserves have been shown to increase both abundance and biomass (Aburto-Oropeza et al., 2011; Williamson et al., 2004) whereas in invertebrates, reserves have been shown to lower size and have little effect on biomass (Halpern, 2003). Our results fit neither of these 'reserve' models, instead suggesting deviation from energetic equivalence in the local-size density relationships (White et al., 2007); patterns that could be driven by size asymmetries in competition for resources (e.g. Munger and Brown, 1981; Russo et al., 2003) or differences in the availability of resources to different size species (Ernest, 2005; Holling, 1992).

Over the course of the study, photosynthetic yield (ϕ) was found to increase in all treatments at all sites over time and at a faster rate in areas where grazers were excluded suggesting herbivory is playing a direct role in suppressing photosynthesis (Nabity et al., 2009; Qiang and Richmond, 1996). Analysis of the algal community composition indicated that the exclusion of grazers supported increased algal colonisation, especially that of ephemeral algae, most likely due to their release from direct grazing pressure (Steneck, 1982; Wanders, 1977). Previous studies have shown that overgrowth of bleached CCA by other

algal species when grazers are removed can facilitate colour restoration and photosynthesis by providing shade (Figueiredo et al., 2000; Irving et al., 2004). Wetherbee and Verbruggen (2016) argue that this allows the re-distribution of metabolites from uncovered to shaded portions of the thallus. Improvement in photosynthetic capacity, was not however, linked to an increase in areal extent of healthy CCA despite a decrease in the percent cover of bleached CCA (which occurred at a similar rate irrespective of location or treatment) suggesting a temporal increase in photosynthetic yield, perhaps driven by a seasonal increase in light intensity (Qiang and Richmond, 1996). In fact, the extent of healthy CCA was shown to decline at the open access site when predators were excluded. The presence of macroalgal stands can create a photosynthetic deficit caused by light attenuation, resulting in a lack of energetic capacity to drive calcification, pigmentation and maintain levels of defence production. This can mean a physical disconnect between the photosynthetically-active portions of the thallus, leading to a decrease in spatial extent when compared to patches left connected to unshaded (not overgrown) thalli (Bulleri, 2006). Here, the failure of bleached CCA to transition back to healthy CCA coupled with a reduction in the overall spatial extent of patches despite some recovery of photosynthetic potential suggests that photosynthetic performance and its role in sustaining tissue metabolic activity is not a principal constraint upon spatial dominance.

The density and size of grazers has been recognised as an important determinant of algal community composition on these shores (Cattaneo and Mousseau, 1995) and is not a new concept having been shown in numerous studies (e.g. Kordas et al., 2017; Sousa, 1979). Here, differences in grazer assemblage structure among sites likely contributed to the change in spatial dominance of CCA over time and ultimately change in community composition. Relationships among sessile functional groups were stronger in the presence of grazers (Bertness and Callaway, 1994; Cavieres and Badano, 2009), especially at the no-take and managed access site where grazer densities were lower. The absence of large grazers and/or increase in density of small grazers at the open access site led to a general weakening of these relationships. Indeed, change or reversal of competitive hierarchies mediated by herbivores has been shown in a number of previous studies (e.g. Lubchenco and Menge, 1978; Steneck et al., 1991) and is reinforced here. In this system, the presence of grazers seems to have a particularly strong role in ensuring a positive correlation between bleached CCA and healthy

CCA cover with both articulated and corticated species of algae and avoiding overgrowth by ephemeral algae. Grazer-induced bioerosion has been also shown to reduce percent cover of CCA (O'Leary and McClanahan, 2010), although here, the exclusion of grazers using cages has had no impact on preventing the loss of CCA cover over time suggesting bio-erosion is not influencing CCA areal extent here. When grazers were excluded, there were marked shifts toward a few strong negative correlations, particularly between bleached CCA and corticated and ephemeral algae, and reduction in relative importance of crustose algae and filter-feeding organisms (non-calcareous crustose algae is often prevalent in areas of high grazing pressure; Duffy and Hay, 1990; Jara and Moreno, 1984).

It is well known that CCA plays an important role in the population growth and development of species that depend on CCA as a substrate for colonisation (Huggett et al., 2005; Tahil and Dy, 2016) and as part of their diets (Asnaghi et al., 2015; Maneveldt et al., 2006). The persistence of healthy CCA is likely to underpin the persistence of higher trophic levels and species important to humans. Activities that lead to the removal of canopy-forming algae that protect CCA from harmful UV radiation, or grazers that prevent overgrowth by ephemeral algal growth, should be carefully considered (Ojeda and Santelices, 1984). Here, persistence of CCA was observed only at the managed access site (EQ), where grazers played an important role in preventing overgrowth. Surprisingly, similar facilitation by grazers was not observed in the adjacent no-take marine reserve, where fleshy crustose algae (predominantly Hildenbrandtia) appeared to obtain greater benefits. At the open access site, it could be argued that large grazers are removed by humans to the extent that they are in such critically low abundance that they are unable to prevent overgrowth of CCA by other algal species. Elsewhere, the removal of grazers by humans when sufficiently widespread can lead to species becoming critically endangered (e.g. *Patella ferruginea*, Coppa et al., 2016). However, differences in grazer population structure among sites defined by different levels of management led to the emergence of different communities, especially when grazers were excluded. Interestingly, it was at the managed access site (El Quisco) where the greatest percentage cover of bleached CCA occurred which suggests a disproportionately important role of larger grazers (rather than density) in algal herbivory and structuring of intertidal communities.

This study supports the proposition that under certain conditions, interactions that are typically considered competitive (negative) may become facilitative (Bertness and Callaway, 1994). Specifically, ephemeral and corticate algae that often compete with CCA appear to positively influence colour restoration of bleached CCA. The health of CCA in areas of pulse environmental perturbations may therefore be reliant on the buffering capacity of certain macroalgal species to mitigate environmental stress. Those interactions, however, appear strongly mediated by the population structure of grazers (Lindberg et al., 1998). Unlike other studies, our results show that an absence of large grazers can lead to overgrowth and shading of CCA by macroalgae leading to a decrease in percent cover and replacement by other species. This balance is likely determined by the density, and probably, species-specific size distributions of grazing species which may be influenced by the level of harvesting. Given that CCA plays an important role in the population growth and development of species that depend on CCA as substrate or food (Asnaghi et al., 2015; Huggett et al., 2005; Maneveldt et al., 2006; Tahil and Dy, 2016), consideration of how harvesting might change the population structure (density and size) of grazers and the consequential changes in the functioning of lower trophic levels is needed in any decision to implement conservation management tools such as MPAs.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2019.03.003.

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